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ABSTRACT

The incorporation of mathematical modeling experiences into an undergraduate biology course is described. Detailed expositions of three models used to teach concepts of population ecology are presented, including introductions to major concepts, user instructions, trial data and problem sets. The models described are: 1) an exponential/logistic model of population growth; 2) a competition model; and 3) a model of the Lotka-Volterra predation equations for a system of two interacting predators. Some reasons for the increased use of mathematical modeling and systems theory are sketched, and the points are made that early exposure to mathematical modeling helps students to see the relationships between models and the real world, enables them to grasp the relevance of mathematics to biology, and gives them an introduction to important theoretical ideas. Finally, the ideal model is described as one which is consistent, clear in its directions to students, and rapid in response to input. (PB)

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TEACHING POPULATION ECOLOGY MODELING BY MEANS OF THE HEWLETT-PACKARD 9100A

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The utilization of mathematical modeling and systems theory in modern ecology is becoming rapidly apparent for several reasons. First, there has developed a rather substantial body of literature in operations theory in the physical sciences and especially engineering. The mathematics of linear systems, at least, are well-behaved and quite useful. Secondly, the availability of computing devices of all sizes and capabilities has made mathematical modeling at some level a practicable program for most colleges. In the third place, we can point to the historical development of ecology as a science from its inception in the 1860's to the present. Much of the early work was descriptive, observational and could be called systematized natural history. As time passed, empirical data from inductive studies accumulated and theories began to merge to organize these data into meaningful concepts. As these theories became at least tentatively accepted, the desire grew to test them broadly in new locations and different conditions. Thus, ecology had shifted from inductive to deductive thinking and principles existed which could be tested. Finally, it might be pointed out that the 1960's and 1970's have seen concern for environmental problems become a major fact of public life. The need for solutions, or at least approaches, was urgent and the luxury of inductively derived principles and an exhaustion of possible cases no longer existed. The technique of mathematical modeling, however, provided a means of looking at possible solutions to environmental problems without extensive, long-term data collection.

Recent textbooks in ecology [1], [2], have reflected the influence of mathematical models and other quantitative techniques. The main purpose of this paper, however, is to illustrate how mathematical modeling experience can be incorporated into the lower division general biology course. Our course is offered to sophomore biology majors who usually have a year of college chemistry and possibly a year of mathematics. We have used the book Central Concepts of Biology [3] which is rather ideally oriented toward the mathematical modeling approach in population biology.

An exposure to mathematical modeling has several values to the students in this course. First, students have seldom failed to grasp conceptually the relationships between models and the "real world" that is being modeled. They do not, of course, see many of the implications of this conception, but they have a working knowledge of how scientists make assumptions, formulate hypotheses and then test them. Ideally, the student would be able to use the model in conjunction with an actual laboratory experiment and modify the model in interaction with actual measurements, but this is not usually possible with lower division students, so the facts are generally contrived or taken from previously published data.

Secondly, mathematical modeling provides an opportunity to incorporate mathematics into the biology curriculum at an early stage in such a way that students are able to see the relevance of it and utilize their required mathematical training. In doing this, the biology teacher is able to give an accurate reflection of what professional ecologists do. A third way in which mathematical moleing may have value to the student of ecology is that he will be exposed to the important theoretical ideas of such investigators as Lotka, Volterra, and Gause from earlier times, and enables him to get some understanding of the contribution of such important modern theorists as Watt [4], Holling [5], and Patten [6]. In the broader environmental concerns the exposure of modeling gives students an appreciation of the work of Forrester [7] and Meadows et al. [8]. Such appreciation should enable students to become more quickly involved in the approaches that are being taken to the solution of current environmental problems.

The significant involvement of students in mathematical modeling at the sophomore level seems to involve several factors. The concepts that are to be modeled need to be presented clearly and in our case we have done this via the assigned reading in Baer et al. [3], and by supplementary materials to be shown later. We have developed three models which correspond to a large section of the material in the Baer text: (a) exponential/logistic model of population growth, (b) competition model and (c) Lotka-Volterra predation equations for a system of two interacting predators. In addition to clearly presenting the concepts associated with the models, students need to have essentially free access to computing facilities to operate the models without pressure. At our institution a system similar to

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the reserve book system in the library is used, in which students check out the key to the computing laboratory during library hours.

Our experience with models has indicated that for optimum effectiveness: (a) there must be consistency in notation, parameters, etc., throughout all materials used with the models, (b) the "user instructions" must be clear, since the students are not expected to know how to program or analyze a program, (c) the output from the model must be rapid and understandable since students quickly become discouraged when iterations require large amounts of time, and (d) the manipulation of the model expected of the students should be clearly stated.

With each of the models, the student receives a written introduction to the concepts involved, user instructions, and trial data and problem set. The student materials for the three models mentioned above are reproduced below.

EXPONENTIAL/LOGISTIC POPULATION GROWTH

Exponential growth curve (see Figure 1)

The growth of a population "when unchecked"--to use Malthus' phrase--is very simply, though incompletely, represented by the graph on the next page. With the passage of time, an unchecked (exponentially growing) population increases faster and faster. The units on the axes of the graph vary depending on the organism of interest; e.g., years for humans, days for fruitflies, minutes for bacteria, etc. In cybernetic terminology (cybernetics = the science of communication and control in complex systems), reproduction is positive feedback if environmental influences are not considered. That is, the input to the system (reproducing organisms) receives NO negative data from the output (new individuals) which informs it that what it is producing or doing is disfunctional to the system. Children have more children and these in turn produce more children. THE REPRODUCTION OF AN UNCHECKED POPULATION IS LIKE MONEY INVESTED AT COMPOUND INTEREST. The assumption that the interest is compounded only once a year is unrealistic, but the resulting figure is still a close approximation of population size. For a more exact treatment another equation is available, one which assumes continuous increase, continuously compounded:

The Equation is: $N_t = N_o e^{rt}$ or $\ln N_t = \ln N_o + [(r)(t)]$ (1)
where:

N_t = final population
N_o = initial population
r = intrinsic rate of increase (birth rate--death rate)
t = time (in proper units)
e = base of natural logarithms

Unchecked population growth follows the predictions of the function, $N_t = N_o e^{rt}$, and is therefore said to be Exponential Growth (what Malthus called geometric growth).

Logistic growth curve (see Figure 1)

All populations allowed indefinite exponential growth will eventually contain more organisms than there are atoms in the visible universe, and whose combined bulk will be expanding outward at the speed of light. Of course populations do not have this capacity and exponential growth cannot continue indefinitely.

In noting the conditions for exponential population growth we assumed that birth and death were constant. Let us now examine, in a more realistic way, what the effects of increasing population size might be on the birth rate and death rate. As the population increases, the death rate will probably increase due to a number of effects, such as reduction in the average food and space available to each individual. The birth rate, on the other hand, will probably decrease with increased population size, except perhaps for small populations in which individuals are spaced so far apart they have trouble finding mates.

The logistic growth curve is a mathematical model of population growth when the effect of N on birth rates and death rates are taken into account. One form of this equation and its solution (as a curve) are shown.

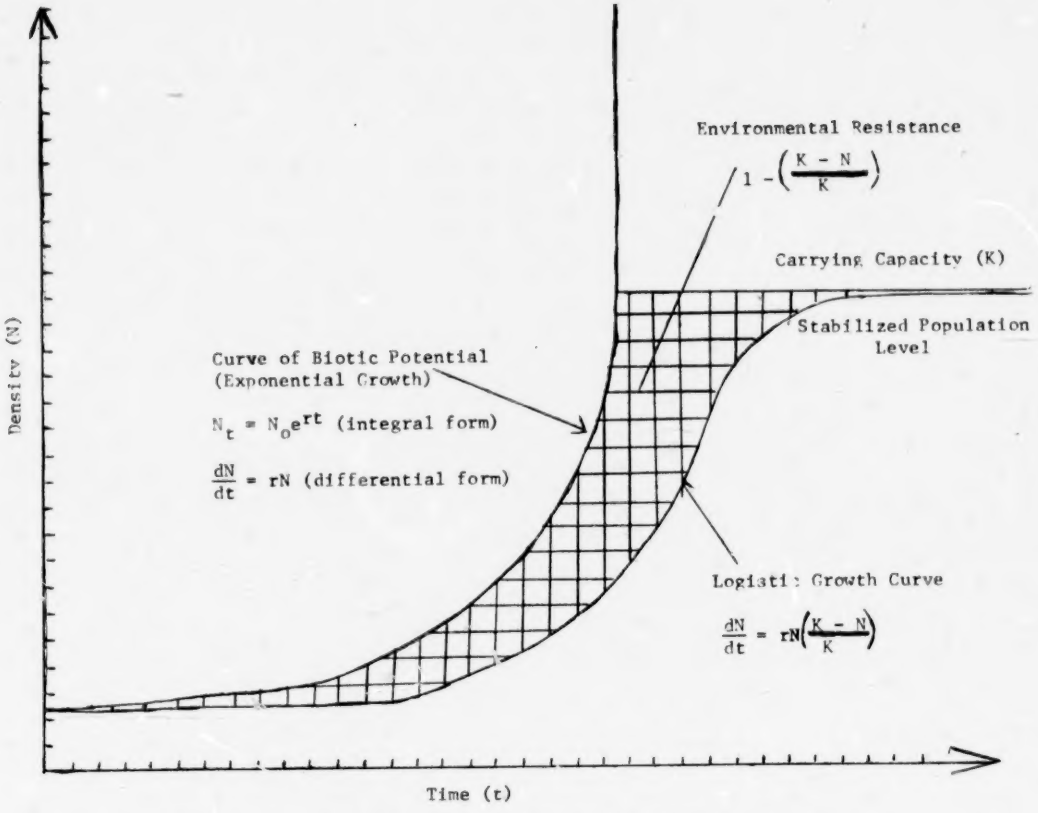

Figure 1. Exponential and Logistic Growth Curves

Biotic Potential (r) = the ability of a population to grow, ignoring environmental limitations. This quantity is therefore theoretical and each species has a unique r. It is also called "instrinsic rate of natural increase."

Environmental Resistance (proportional to (1/(K-N/K)) or 1 - (K-N/K)) = the resistance imposed when some environmental factor or factors becomes limiting and decreases the birth rate or increases the death rate, or both.

Carrying Capacity (K) = the limit to biotic potential of a particular species population size imposed by environmental resistance under a given set of conditions.

Logistic Growth Curve (see above) = a curve produced by combining the biotic potential and environmental resistance. It is, more specifically, the product of the two. Many populations appear to grow as predicted by the logistic growth curve, but it is possible to produce a sigmoid of S growth curve by using other mathematical expressions.

Exponential Population Growth

On the following page are the "User Instructions" for a program, concerning exponential population growth, which the Hewlett-Packard 9100A Desk Computer will execute.

The program is based on our old friend $N_t = N_o e^{rt}$. We will use the differential form of the equation, however, and arrive at the new population size in the following way,

$$\frac{dN_1}{dt} = rN_1$$

$$dN_1 = rN_1 dt \quad \left(\text{where } r = \left(\frac{dN}{dt}\right) / N\right)$$

$$N_2 = N_1 + rN_1 dt$$

When we do this we are simulating on a computer the exponential growth of a population. The size of the projected population is evaluated at each specified time increment in the simulation.

Two situations can be analyzed using this program. It is thought that these are the ones most often encountered in terms of available demographic statistics.

Situation One:
Given:
1) intrinsic rate of national increase, r
2) present population size, N_1

Situation Two:
Given:
1) population at some time in the past, N_o
2) population now, N_1
3) time point in past (corresponding to N_o), t_o
4) time now (corresponding to N_1), t_1

In situation one, if you supply r and N_1 and dt (the time increment of projected population growth) the program will calculate a projected population size (N_2) at each time increment into the projected future. This projected growth is based on the intrinsic rate of natural increase (r) and present population size (N_1) which you supply.

In situation two the only data which you possess are the population size now (N_1), the population size at some time in the past (N_o) and dt (same as above). If you enter these data correctly into the program, the intrinsic rate of increase (r) will be calculated based on the time period you have data for. This calculated r will be used to project the population into the future. Thus you are able to make a conclusion such as this: "Based upon population growth between 1950 and 1960, the population of this area in 1980 will be _____." Of course, this projected population is subject to the assumptions of the exponential growth model.

Now look at the "User Instructions" and see if it is clear to you how to analyze these two situations with the program.

User Instructions: Exponential/Logistic Population Growth

ENTER PROGRAM
PRESS: GO TO (0) (0)
PRESS: CONTINUE
DISPLAY: X-1, Y-0, Z-0
ENTER: T→X
PRESS: CONTINUE
DISPLAY: X-2, Y-0, Z-0
ENTER: N_0→X
PRESS: CONTINUE
DISPLAY: X-3, Y-0, Z-0

Is r known?

NO

ENTER: t_1→X
PRESS: CONTINUE
DISPLAY: X-4, Y-0, Z-0
ENTER: t_2→X
PRESS: CONTINUE
DISPLAY: X-5, Y-N_1, Z-0
ENTER: t_3→X
PRESS: CONTINUE
DISPLAY: X-6, Y-N_1, Z-N_1
ENTER: N_0→X
PRESS: CONTINUE

YES

ENTER: r→X
PRESS: CONTINUE
DISPLAY: X-7, Y-0, Z-0
ENTER: DT→X
PRESS: CONTINUE
DISPLAY: X-8, Y-0, Z-0

EXPONENTIAL OR LOGISTIC?

LOGISTIC

ENTER: K→X
PRESS: CONTINUE
DISPLAY:

N_2	Z
T	Y
r	X

EXPONENTIAL

ENTER: 0→X
PRESS: CONTINUE
DISPLAY:

N_2	Z
T	Y
r	X

THESE DISPLAYS WILL CONTINUE TO FLASH, UNTIL USER STOPS BY PRESSING PAUSE

Problems: Population Growth

1. Solve equation 1 for r.
2. Solve equation 1 for t.
3. What would be the gereral expression for doubling time, t_2?
4. Assume the present population of the United States is 204 million. What will the population be in the year 2000 if the population grows at a rate of 1.0% per year?
5. The population of Santa Barbara County can be assumed to be growing at a rate of 1.3% per year. The present population is about 265,000. When will the population reach 500,000? Will Santa Barbara County be overpopulated? Why?
6. A Central American country is growing at 3.8% per year. Assume some hypothetical population figures and calculate the doubling time. Does the size of the population influence the doubling time? How?
7. Assume the "standing room" for a human being is an area of 60 cm. by 30 cm. What would be the standing room population of the land area of the world? (Land area of the earth=148.847 x 10^6 km^2).

8. Assume that the present world population is 3.6×10^9 (3.6 billion), and that the rate of increase is a uniform 2% per annum, without acceleration. How long will it be before there is standing room only?

9. California recently passed the 20×10^6 (20 million) mark in population. California has an area of approximately 4.1×10^5 km^2. How will the area per person (density) diminish between now and the year 2000 if the population increases at 1.0% per year? What are the implications of this change?

10. List and briefly defend all of the factors that you think are important in trying to make an estimate of the optimum world population. Now, using those factors make such an estimate. Is the earth presently overpopulated?

11. In a rapidly expanding, continuously breeding population of human lice, r was calculated to be 0.111 per day. What is the rate of increase of a population of 100 lice?

12. By 1959 the human population had reached 2,907,000,000 and was growing even faster than in earlier times. On a world-wide basis, the birth rate was 36 per thousand persons per year and the death rate was 19 per thousand persons per year. What was the rate of population increase in 1959?

13. When Norway rats invade a new warehouse where living conditions are ideal, they multiple at a very rapid rate: r=0.0147 per day. How many days are required for each doubling of the population size?

14. Below is a table giving the population of California at 10 year intervals and its rank in population among the several states:

Year	California Populations (N)	Rank	ln N	r
1920	3,426,861	8		
1930	5,677,251	6		
1940	6,907,387	5		
1950	10,586,223	2		
1960	15,717,204	2		
1970	19,953,134	1		

a. If you base population projections on the growth rate between 1920 and 1930, was the population in 1970 greater or smaller than you would expect?

b. On the same graph plot numbers versus time and ln of numbers versus time. How do the two curves relate? Why?

c. Now on the just-completed graph plot r for each 10 year period. Did the growth rate increase or decrease or remain constant during the period 1900-1970?

15. Below is a table showing the population sizes of selected counties in the United States.

County	Population 1960	Population 1970	r	Population 2000
Mohave, Arizona	7,736	25,857		
San Miguel, Colorado	2,944	1,949		
Stanley, South Dakota	4,058	2,457		
Virginia Beach, Virginia	8,091	172,106		
Santa Barbara, California	168,962	264,324		

a. Calculate r for each population for the 10 year interval.

b. Using the calculated r and the 1970 population size, project the population to the year 2000 using 1 year iteration intervals.

16. Write a paragraph describing the values and pitfalls of analyses and projections of population such as that above. What are the assumptions? What important factors are not included? etc.

Bonus

17. Prove analytically that in the case of pure logistic growth the optimal yield occurs when N=k/2. (This requires a knowledge of elementary calculus).

MATHEMATICAL MODEL FOR COMPETITION

Competition is an important type of interaction between populations. That competition has received so much attention is not surprising, in view of the importance given it by Darwin, who refers to "the infinitely various ways beings have to obtain food by struggling with other beings, to escape danger at various times of life, to have their eggs or seeds disseminated etc., etc." In this list, competition appears first. Competition may be defined as interaction between populations in a common environment which share a limited resource, such a food or nest sites. As for predation, a number of different approaches have been used to analyze competition. One of these is analysis utilizing a simple mathematical model.

The model suggested by Gause for competition between two species is given in the box below. These equations are derived from the logistic model of population growth. They take into account the depression of logistic growth caused by interspecific competition. The simultaneous equations may be expressed in words as

[change in number of first species per unit time in the mixed population] = [intrinsic rate of increase of first species] x [degree to which the potential increase has been realized]

[change in numbers of second species per unit time in the mixed population] = [intrinsic rate of increase of second species] x [degree to which the potential increase has been realized]

$$\frac{\Delta N_1}{\Delta t} = r_1 N_1 \quad \frac{k_1 - N_1 - \alpha N_2}{k_1}$$

$$\frac{\Delta N_2}{\Delta t} = r_2 N_2 \quad \frac{k_2 - N_2 - \beta N_1}{k_2}$$

where:

N_1=numbers in population 1
N_2=numbers in population 2
r_1, r_2=intrinsic reproductive rates of the two populations
k_1, k_2=carrying capacities of the environment for the two populations
α= the competition coefficient showing the relative effect of an individual of N_2 on N_1, compared to the effect of N_1 on N_1.
β = competition coefficient, showing relative effect of N_1 on N_2.

The assumptions upon which this model is based include, of course, the same cones which the logistic growth curve is based upon: (1) all organisms are equivalent, (2) responses of the population to change occur instantaneously and (3) the upper limit--the carrying capacity, K--remains constant. (note that in the solution for the general conditions for the outcome of competitition only the saturation values, K_1 and K_2, and the competition coefficients appear (cf. pp. 63-64 in Slobodkin). This implies that, at least in a formal sense, the intrinsic rate of natural increase is not of significance in determining the outcone of competition in a constant environment).

In competition, each species decreases the degree of realization of its growth potential at of the competing species. That is, four processes hinder population growth:

2. increase in numbers of the second species hinders the growth of the first,

3. increase in numbers of the second species hinders its own growth, and

4. increase in numbers of the first species hinders the growth of the second.

References: Competition Model

1. A. S. Baer, W. E. Hazen, D. L. Jameson, and W. C. Sloan, Central Concepts of Biology. New York: The Macmillan Company, 1971. (Chapter 18: pp. 265-270).

2. L. B. Slobodkin, Growth and Regulation of Animal Populations. New York: Holt, Rinehart and Winston, 1961, (Chapter 7: pp. 62-81.)

3. E. O. Wilson and W. H. Bossert, A Primer of Population Biology. Stamford, Connecticut: Sinauer Associates, 1971. (Chapter 3: pp. 156).

User Instructions: Competition Model

ENTER PROGRAM
PRESS: GO TO (4) (3)
ENTER: $K_1 \rightarrow X$
PRESS: CONTINUE
ENTER: $K_2 \rightarrow X$
PRESS: CONTINUE
ENTER: $\alpha \rightarrow X$
PRESS: CONTINUE
ENTER: $\beta \rightarrow X$
PRESS: CONTINUE
ENTER: $r_1 \rightarrow X$
PRESS: CONTINUE
ENTER: $r_2 \rightarrow X$
PRESS: CONTINUE
ENTER: $N_2 \rightarrow X$
PRESS: CONTINUE
ENTER: $N_1 \rightarrow X$
PRESS: CONTINUE
ENTER: $T \rightarrow X$
PRESS: CONTINUE
PRESS: CONTINUE
ENTER: $DT \rightarrow X$
PRESS: CONTINUE
→DISPLAY:

N_1	Z
T	Y
N_2	X

THIS DISPLAY WILL CONTINUE TO FLASH, UNTIL USER STOPS BY PRESSING PAUSE.

PRESS: PAUSE (TO STOP FLASHING AND RECORD VALUES)

└PRESS: CONTINUE (TO OBTAIN FURTHER VALUES)

NOTE: RUN THE MODEL UNTIL 1) STABLE VALUES FOR BOTH POPULATIONS ARE ACHIEVED OR 2) ONE POPULATION IS ELIMINATED (=0).

Problems: Competition Model

The following values will give a relatively stable situation in which neither of the two competing species is eliminated:

t =0.00
dt=0.10
N_1=39.0
N_2=77.0
K_1=100.0
α=0.25
r_1=0.57
K_2=200.0
β=0.10
r_2=0.34

1. Plot numbers versus time for S_1 (species 1) and S_2 on the same graph for the above initial date. (Use millimeter graph paper.)

2. Manipulate the initial data (above) in such a way that you have the following three situations.

   a. $K_2 > K_1/\alpha$ and $K_2/\beta > K_1$

   b. $K_1/\alpha > K_2$ and $K_1 > K_2/\beta$

   c. $K_2 > K_1/\alpha$ and $K_1 > K_2/\beta$

3. Graph each of the above cases (a, b, and c) in the same manner as you did in problem 1.

4. Write an explanation of what you think is happening in <u>each</u> of the four cases you have studied. (i.e., problem 1 and 2). Address yourself to the following questions:

   a. What are the conditions for equilibrium between two competing species? (You should be able to state this in precise mathematical terms).

   b. What happens when you manipulate the various parameters? (i.e. dt, N_1, N_2, K_1, r_1, r_2, α, β).

   c. How do you relate what you have found to the basic equations describing logistic growth of S_1 and S_2 when they are competing?

LOTKA-VOLTERRA PREDATION EQUATIONS FOR A SYSTEM OF TWO INTERACTING SPECIES

Introduction (taken from Baer, et al. 1971 Central Concepts of Biology. Macmillan.)

In examining the phenomenon of predation, a number of different approaches have been used: (1) mathematical studies, which derive a quantitative relation from a number of very simple assumptions; (2) experimental studies, where organisms suitable for the laboratory have been grown under more or less constant conditions; (3) studies in nature; and (4) some combinations of these methods.

A simple mathematical model for predation is illustrated by the Lotka-Volterra simultaneous equations which give the change in population size of two species, the predator and the prey (see box below). The equations are derived from the logistic model of population growth. The simultaneous equations characteristics of the predator-prey relation can also be expressed as:

change in number of prey per unit time	=	intrinsic increase of prey per unit time	=	destruction of prey by predator per unit time
change in number of predators per unit time	=	increase in number of predators per unit time as a result of eating prey	=	death of predators per unit time

LOTKA-VOLTERRA PREDATION EQUATIONS FOR A SYSTEM OF TWO INTERACTING SPECIES

$$\frac{N}{T} = r_1N_1 - k_1N_1N_2 \qquad \text{and} \qquad \frac{N_2}{T} = k_2N_1N_2 - d_2N_2$$

where:
N_1=number of individuals in prey population
N_2=number of individuals in the predator population
T=time
r_1=intrinsic rate of increase of prey population
k_1=predation rate; the likelihood of a predator catching and eating a prey
k_2=conversion rate at which prey substance is converted to new predators
d_2=the natural death rate of the predator

The assumptions upon which the model is based include most importantly that (1) the growth of each population is not affected by its size; (2) the environment is unlimited; (3) the likelihood of a predator eating a prey is independent of the density of either species; and (4) all effects are instantaneous. The unreasonable nature of these assumptions shows how unlikely it is that the model can be applied to nature in detail.

When the two equations are solved simultaneously, an intrinsic cyclic relation is revealed, one species being at maximum size when the others is at a minimum.

References: Predation Model

1. A. S. Baer, W. E. Hazen, D. L. Jameson, and W. C. Sloan, Central Concepts of Biology. New York: The Macmillan Company, 1971. (Chapter 18: pp. 258-265).

2. C. J. Krebs, Ecology: The Experimental Analysis of Distribution and Abundance. New York: Harper and Row, 1972. (Part 3: Chapter 13).

3. L. B. Slobodkin, Growth and Regulation of Animal Populations. Holt, Rinehart and Winston, 1961, (Chapter 13: pp. 143-151).

4. E. O. Wilson, and W. H. Bossert, A Primer of Population Biology. Sinauer Associates, Inc., Samford, Connecticut. 1971 (Chapter 3: pp. 127-138).

User Instructions: Predation Model

PRESS: GO TO (0) (0)
PRESS: CONTINUE
DISPLAY: 0.....Z
0.....Y
1.....X
This display will be similar until 8 model parameters have been entered; i.e. numbers 1-8 will appear in the X register indicating that initial data should be entered.
ENTER: N1→X(1)
PRESS: CONTINUE
ENTER: N2→X(2)
PRESS: CONTINUE
ENTER: dt→X(3)
PRESS: CONTINUE
ENTER: K1→X(4)
PRESS: CONTINUE
ENTER: K2→X(5)
PRESS: CONTINUE
ENTER: D2→X(6)
PRESS: CONTINUE
ENTER: T→X(7)
PRESS: CONTINUE
ENTER: R1→X(8)
PRESS: CONTINUE
PRESS: PAUSE
DISPLAY: $N2_1$.....Z
$N1_1$.....Y
t_1.....X
PRESS: CONTINUE
PRESS: PAUSE
DISPLAY: $N2_2$.....Z
$N1_2$.....Y
t_2.....X

PRESS: CONTINUE (until values become unrealistic (negative or less than one) or user decides to terminate the simulation).

Problems: Predation Model

PLEASE NOTE THAT RELATIVELY STABLE PREDATOR-PREY OSCILLATIONS OCCUR WHEN THE FOLLOWING VALUES ARE USED AT APPROPRIATE POINTS IN THE "USER INSTRUCTIONS":

N1=20.0
N2=4.0
dt=0.10
K1=0.10
K2=0.02
D2=0.50
T=0.0
R1=1.0

(C. F. Krebs, 1972, Ecology: The Experimental Analysis of Distribution and Abundance. Harper and Row, Publisher)

1. What do each of the symbols above signify?

2. Graph (N vs T) the predator-prey oscillations when the above data serve as the initial values of the system. (Use millimeter graph paper)

3. Describe in words what the graph means in terms of a biological system (e.g. mountain lions and deer, moths and birds, etc.)

4. Write a paragraph indicating the effect on stability of the predator-prey system when each of the following simulations are performed (i.e. hold all other values the same and.....)

1-double size of prey population
2-halve size of prey population
3-double size of predator population
4-halve size of predator population
5-set dt=1.0
6-set dt=0.05
7-double K1
8-halve K1
9-double K2
10-halve K2
11-double D2
12-halve D2
13-set R1=0.1
14-set R2-0.5
15-Do any two odd numbered things at the same time, keeping all other values at original levels.
16-Do any two even numbered things at the same time, keeping all other values at original levels.

5. Write a short essay describing relationships between predators and their prey based upon the behavior of this model.

NOTES AND REFFRENCES

1. E. P. Odum, Fundamentals of Ecology. (2nd ed.) Philadelphia: W. A. Saunders and Co., 1971.

2. C. J. Krebs, Ecology: The Experimental Analysis of Distribution and Abundance. New York: Harper and Row, 1972.

3. A. S. Baer, W. E. Hazen, D. L. Jameson, and W. C. Sloan, Central Concepts of Biology. New York: The Macmillan Company, 1971.

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